

THE EFFECT OF RECIPROCAL DIFFERENCES ON THE GENETIC COMPONENTS
OF VARIATION IN A FIVE-PARENT DIALLEL CROSS OF COMMON WHEAT
(*TRITICUM AESTIVUM* L.)*

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Abstract

The effect of significant reciprocal differences on the genetic components of variation was studied through diallel cross analysis of five-parental F₂ diallel table in common wheat (*Triticum aestivum* L.). The characters studied were number of spikes per spike, 1000-kernel weight (in grams) and the yield of grains per plant (in grams). The F₂ diallel table was divided into two sub-sets of five arrays each, one by keeping the female parent constant and the other by treating the male parent constant.

The results reveal that partitioning the F₂ diallel table into two such sub-sets affects the array variances (V_r) and the array parent-offspring covariances (W_r). This effect is reflected in the position of the parents with respect to order of dominance and proportion of negative and positive effects of genes, for all the characters studied. Additive components of variation (D and h_2) remain unaffected.

Introduction

The publications of Hayman (1954 a,b) and Jinks (1954, 1956) with respect to theoretical considerations of quantitative genetic analysis of diallel crosses have provided geneticists and plant breeders with an elegant method of assessing the quantitative genetic structure of parental lines. By virtue of its systematic approach in breeding procedures and over-all genetic evaluation from biometrical-genetic analysis, the diallel cross technique has been enthusiastically used in almost all kinds of plant breeding programmes. The over-all genetic evaluation of the quantitative characters considered, comes from the values of genetic components of variation viz., D , H_1 , H_2 and F . By means of these parameters the mean degree of dominance, the proportion of dominant to recessive genes in the parents and the coefficient of correlation between the parental order of dominance and parental measurements can be estimated. The W_r , V_r graphical analysis, if supplemented with statistical genetic analysis, reveals the type of non-allelic interaction and categorizes the parents into those with dominant and those with recessive genes controlling the particular character.

The application of the diallel cross in wheat (*Triticum aestivum* L.) started with the work of Whitehouse *et al* (1958) who studied the behaviour of 19 spring wheat varieties with respect to yield and its components. Crumpacker & Allard (1962) made a detailed study of diallel analysis of heading date over a three years period in 10 spring cultivars. Bagnara (1967) and Kaltsikes & Lee (1971) in durum wheats; Gyawali *et al* (1968), Fonseca & Patterson (1968) and Bizer *et al* (1971) with winter wheats; Knott & Sindagi (1969), Walton (1969), Hsu & Walton (1970), Bhatt (1971) and Paroda & Joshi (1970) in spring wheats have studied the genetics of yield and its various components by means of diallel cross analysis.

The studies reported in this paper concern the analysis of yield and its components under conditions in which the assumption of 'no differences between reciprocal crosses' is invalidated. Hayman's procedure (1954a) suggests that, in the presence

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of significant differences between reciprocal crosses, the off-diagonal cells of the diallel table should be replaced by the common means of the pertinent crosses and their reciprocals before the analysis is carried out. Instead of following the Hayman procedure (1954a) of replacement, we have divided diallel tables, for yield and its components into their maternal and paternal orthogonal reciprocal sub-sets of five arrays each in order to compare the magnitude of reciprocal effects before performing the analysis. The purpose of the present investigation was to determine the extent to which the components of variation and genetic parameters are affected by the non-equivalence of reciprocal crosses in the diallel cross.

Materials and Methods

Five spring wheat varieties; Marquis (M) and Chinook (CH) from Canada, Khush-hal (K) from Pakistan, and Ciano and Inia [(C) and (I)] from Mexico were used in a complete diallel crossing in 1970-71. In the winter of 1971 all F_1 's, together with their reciprocals, were grown in the propagation rooms under controlled conditions, to get their F_2 generation. In the spring of 1972, this five-parent F_2 -diallel was seeded in a randomized block design with five replications. Each entry was repeated five times in every replication, giving 125 rows for each replication. All entries in each replication were randomized. Each row, 15 feet long, consisted of 30 plants with six inches distance from plant-to-plant and twelve inches from row-to-row. Observations were recorded for number of spikelets per spike, 1000-kernel weight (in grams) and yield of grain per plant (in grams, and hereafter called yield per plant). To determine the number of spikelets per spike and yield per plant, five plants were selected at random from each row in each block and three spikes from each selected plant were randomly scored for number of spikelets. For 1000-kernel weight, four readings were scored at random from the bulked yield sample of every row, giving twenty readings per entry per replication.

For the analysis of the diallel cross, the reciprocal differences were tested following analysis of variance of the diallel table as described by Hayman (1954a). After noticing significant reciprocal differences for each of the characters used (Table 2), we decided to divide the diallel table of each character into two sub-sets orthogonal and reciprocal to each other. The first sub-set of five arrays was produced by keeping the female parent constant and the male parent variable, and the second sub-set by keeping the male parent constant and female variable. The aim of keeping the reciprocal sub-set apart was to evaluate the over-all genetic picture of the inheritance of yield and its components with respect to the extent to which the components of variation and the genetic parameters are affected by the significant reciprocal differences. Individual sub-sets were analyzed for each of the character following Hayman's (1954b) and Jinks (1956) model of diallel analysis. The graphical analysis of each of the sub-sets for the characters considered was supplemented by standardized deviation graphs of parental measurements and $Wr + Vr$, a technique first introduced by Johnson & Aksel (1959). The environmental component of variation was estimated after Aksel & Johnson (1963). In all these analyses, the data have been averaged over five replications.

Experimental Results

The average performances of the five parents and their F_2 hybrids for each of the characters is shown in Table 1.

TABLE 1. 5x5 complete F₂-parent diallel table for number of spikelets per spike (1st reading), 1000-kernel weight (2nd reading), and yield per plant (3rd reading) averaged over five replications.

Female parents	Male parents				
	Marquis	Chinook	Khush-hal	Ciano	Inja
Marquis	16.966	16.677	16.286	15.690	15.874
	36.833	37.552	38.221	37.107	38.290
	26.248	22.839	27.166	22.621	25.358
Chinook	16.459	15.993	15.274	15.480	16.028
	37.641	37.406	39.375	37.364	37.835
	24.818	23.194	26.155	20.898	25.152
Khush-hal	15.410	15.224	14.292	15.518	14.634
	39.835	40.172	43.331	41.207	40.145
	26.968	26.760	28.846	28.707	25.737
Ciano	15.388	14.691	13.992	14.448	15.594
	38.209	36.853	39.876	37.596	37.602
	22.711	20.340	22.853	21.704	20.284
Inja	15.785	15.672	14.188	14.784	13.869
	39.077	37.793	39.280	38.135	38.329
	22.628	23.445	22.371	23.280	19.995

The analysis of variance of the diallel table (Hayman, 1954a) for each of the characters is presented in Table 2.

TABLE 2. The mean squares values and variance-ratio estimates from the analysis of variance of the five parental F₂ diallel-table for yield and its components.

Source of Variation	Characters		
	Number of spikelets per spike	1000-kernel weight	Yield per plant
a	15.1494	57.2969	90.9688
	50.0016**	33.4123**	4.3276*
b	1.1020	2.9187	20.5437
	4.6532**	4.7897**	3.4429**
b ₁	2.0282	0.2897	2.7045
	5.6878	0.2029	1.6528
b ₂	0.9023	2.4580	15.6982
	4.3753**	3.0243*	0.0397
b ₃	1.0766	3.8250	28.0000
	3.7420*	7.5092*	0.9435
c	1.2966	4.4907	29.7358
	3.1796*	8.3899**	3.7874*
d	1.1534	0.4006	9.3346
	3.6410*	0.6226	2.3346

1. First reading under each column refers to Mean Squares and the second to variance ratio (F value).
2. Each component has been tested against its own block interaction.

* Significant at 5% level.

** Significant at 1% level.

Significance of the c component in the analysis of variance indicated significant reciprocal differences for all three characters considered.

Component a, which tests additive gene effects, indicated that for all the characters, the parental lines differed significantly. Component b, which tests dominance effects, was also highly significant for all characters, thus revealing the importance of non-additive genetic system with respect to the specific combinations.

Owing to the presence of reciprocal differences, each diallel table was divided into two sub-sets (as described in material and methods) given in Table 3 and Table 4.

TABLE 3. Average performance of the parents and their F₂ hybrids as arranged in sub-set I by keeping female parent constant and the male parent variable.

Array-I		Array-II		Array-III		Array-IV		Array-V	
M	16.966	CH	15.993	K	14.292	C	14.448	I	13.869
	38.833		37.406		43.331		37.596		38.329
	26.248		23.194		28.846		21.704		19.995
MxCH	16.677	CHxM	16.459	KxM	15.410	CxM	15.388	IxM	15.785
	37.552		37.641		39.835		33.209		39.077
	22.839		24.818		26.968		22.711		22.628
MxK	16.286	CHxK	15.274	KxCH	15.224	CxCH	14.691	IxCH	15.672
	38.221		39.375		40.172		36.853		37.793
	27.166		26.155		26.760		20.340		23.445
MxC	15.690	CHxC	15.480	KxC	15.518	CxK	13.992	IxK	14.188
	37.107		37.364		41.207		39.876		39.280
	22.621		20.898		28.707		22.853		22.371
MxI	15.874	CHxI	16.028	KxI	14.634	CxI	15.594	IxC	14.784
	38.290		37.835		40.145		37.602		38.135
	25.368		25.152		25.737		20.284		23.280

Note : The first, second and third readings under each entry refer to the number of spikelets per spike, 1000-kernel weight and yield per plant respectively.

TABLE 4. Average performance of the parents and their F₂ hybrids as arranged in sub set 2 keeping the male parent constant and the female parent variable.

Array-I	Array-II	Array-III	Array-IV	Array-V
M = 16.966 36.833 26.248	CH = 15.993 37.406 23.194	K = 14.292 43.331 28.846	C = 14.448 37.596 21.704	I = 13.869 38.329 19.995
CHxM = 16.459 37.641 24.818	MxCH = 16.677 37.552 22.839	MxK = 16.286 38.221 27.166	MxC = 15.690 37.107 22.621	MxI = 15.874 38.290 25.368
KxM = 15.410 39.835 26.968	KxCH = 15.224 40.172 26.760	CHxK = 15.274 39.375 26.155	CHxC = 15.480 37.364 20.898	CHxI = 16.028 37.835 25.152
CxM = 15.388 38.209 22.711	CxCH = 14.691 36.853 20.340	CxK = 13.992 39.876 22.853	KxC = 15.518 41.207 28.707	KxI = 14.634 40.145 25.737
IxM = 15.785 39.077 22.638	IxCH = 15.672 37.793 23.445	IxK = 14.188 39.280 23.280	IxC = 14.784 38.135 23.280	CxI = 15.594 37.602 20.284

Note : The first, second and third readings under each entry refer to the number of spikelets per spike, 1000-kernel weight and yield per plant respectively.

Before proceeding to the analysis for genetic components of variation, the validity of other assumptions was checked. The assumptions of 'homozygous parents' and 'normal diploid segregation' were found to be valid from previous records of the parental lines. 'No multiple allelism', 'independent action of non-allelic genes' and 'uncorrelated gene distribution' were checked by the analysis of variance of W_r - V_r entities, for the two sub-sets, and is presented in Table 5.

TABLE 5. Mean squares from the analysis of variance of $Wx-Vr$ for two sub-sets of F_2 -diallel for yield and its components.

Source of variation	D.F.	Number of spikelets per spike	1000-kernel Weight	Yield per plant
Blocks	4	0.106	3.159	51.591
Arrays	4	0.061	0.470	0.601
Error	16	0.032	0.183	17.550

It is seen that none of the array mean squares are significant, and thus the above three assumptions underlying the genetic analysis may be taken as valid.

The second degree statistics calculated for each of the characters for the two sets from Tables 3 and 4 are presented in Table 6.

TABLE 6. Second degree statistics from two sub-sets of diallel table for yield and its components.

Statistic	Number of spikelets per spike		1000-Kernel weight		Yield per plant	
	sub-set I	sub-set II	sub-set I	sub-set II	sub-set I	sub-set II
VOLO	1.7179	1.7179	6.9906	6.0006	12.6246	12.6246
WOLO2	0.0572	0.1787	-0.2203	0.4303	1.2655	2.7018
VIL2	0.3933	0.6223	0.9749	2.1318	2.7241	6.7285
VOL2	0.4438	0.2148	1.8139	0.6570	5.2258	1.1103
(MLI—MLO) ²	0.0800	0.0800	0.0500	0.0500	2.2700	2.2700

The estimates for genetic components of variation, derived by substituting these values of second degree statistics in the appropriate formulae (Hayman, 1954b), are presented in Table 7.

TABLE 7. Estimates of genetic components of variation and genetic parameters for two sub-sets of F₂ diallel table for yield and its components.

	D	H ¹	H ²	F
Number of spikelets per spike	1.4249 ± 0.6031 1.4249 ± 0.7866	2.3005 ± 1.7157 2.7305 ± 2.2378	0.7880 ± 1.4773 1.0440 ± 1.9267	2.8554 ± 1.6302 2.3694 ± 2.1262
1000-kernel weight	6.2606 ± 2.4806 6.2606 ± 3.4012	8.9922 ± 7.0572 11.8986 ± 9.6762	-4.8160 ± 6.0763 4.4392 ± 8.3314	13.9864 ± 6.7054* 11.3840 ± 9.1939
Yield per plant	1.6016 ± 1.5755 1.6016 ± 8.4438	± 10.2008 ± 4.4823* ± 22.4012 ± 24.021	-32.0528 ± 3.8594** 0.4268 ± 20.683	6.9596 ± 4.2589 1.2144 ± 22.824
		(H ¹ ÷ D) ¹	(H ² ÷ 4H ¹)	[(4DH ¹) ₂ + F] / [(4DH ¹) ₂ - F]
Number of spikelets per spike		1.27 1.91	0.085 0.095	8.475 4.010
1000-kernel weight		1.19 1.37	-0.133 0.093	0.785 -0.004
Yield per plant		8.475 4.010	28.451 4.874	13.394 1.225

The first reading under each column refers to sub-set I and second to sub-set II.
*Significant at 5% level **Significant at 1% level.

Table 6 provided 55 statistics (25Vr's, 25Wr's, VOLO' WOLO2' VIL2 VOL2 and (MLJ - MLO)²) and ten constants to be fitted to them (D, 5Fr's, H¹, H², h and E) leaving 45 degrees of freedom to test the significance of the genetic components of variation in Table 7. The results reveal that D is significant for number of spikelets per spike, for sub-set I but not for sub-set II. For 1000-kernel weight, D and F are significant in sub-set I but none of the components are significant in sub-set II. Again for yield per plant, H¹ and H² are significant for sub-set I, but none are significant for sub-set II.

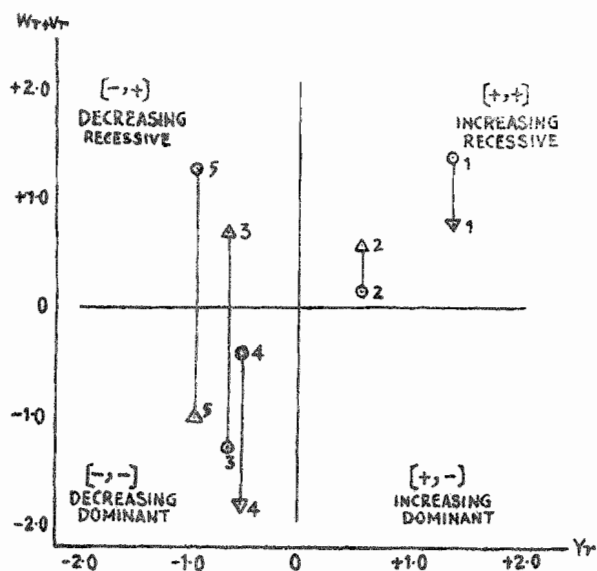


Fig. 1. Standardized deviation graph of parental measurements (Y_r) and order of dominance ($W_r + V_r$) for number of spikelets per spike from two subsets of F_2 -diallel cross.

- = parental Y_r , ($W_r + V_r$) intercepts for sub-set I.
- △ = parental Y_r , ($W_r + V_r$) intercepts for sub-set II.

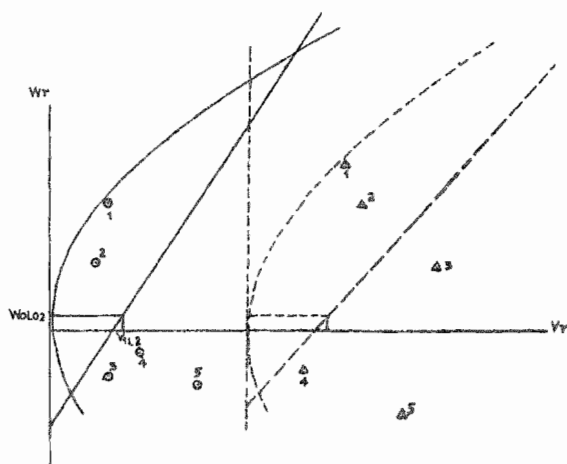


Fig. 2. V_r , W_r graph for number of spikelets per spike from two sub-sets of F_2 diallel cross.

- = V_r , W_r parental intercepts of sub-set I.
- △ = V_r , W_r parental intercepts of sub-set II.

Thus following conclusions could be made:

(1) The mean degree of dominance $(H1 \div D)^{\frac{1}{2}}$ is greater than unity in all cases, suggesting over-dominance as the inheritance pattern of yield and its components. (2) The proportion of genes with positive and negative effects in the parents is $H2 \div 4H1 = 0.085$ for sub-set I and 0.095 for sub-set II in number of spikelets per spike, indicating a strong asymmetry at loci showing dominance. Moreover, the lower values suggest that negative alleles in the parents, responsible for lower number of spikelets per spike, are in excess. In 1000-kernel weight, sub-set I has $H2 \div 4H1 = -0.133$ and for sub-set II it is 0.093. This means that larger proportion of the genes with negative effects is contained by the parents in the sub-set where the male parent has been treated as variable parent and vice-versa. Yield per plant also exhibited inconsistency between the two sub-sets with respect to the proportion of genes with negative and positive effects. (3) The proportion of dominant to recessive genes in the parents is 8.475 and 4.010 for the two sub-sets for number of spikelets per spike and 28.451 and 4.874 respectively for 1000-kernel weight, which means that for these two characters, in both the sets, some of the parents contained more dominant genes than recessive ones. For yield per plant, in the first sub-set some of the parents contained more dominant genes but in the second sub-set, in some of the parents the dominant and the recessive genes were present in equal proportions. (4) Since the parental lines were considered as the recurrent parents in calculating the V_r and W_r values, the value of D will be constant for the two sub-sets.

Discussion

Graphical analysis applied to the data obtained from diallel analysis can greatly supplement the conclusions drawn therefrom by enabling the visual assessment of the parental entries. Thus according to their positions on the graphs, the proportion of dominant to recessive genes, the proportion of negative to positive gene effects and the correlation between the parental order of dominance and parental measurements can clearly be demonstrated.

From the results of Table 2 for number of spikelets per spike, it was concluded that the additive and dominance effects of the genes were highly significant, revealing substantial differences in the parents and their hybrids. Item b2 of Table 2 tests whether the mean dominance deviation characteristic of each hybrid from its respective mid-parent values per array differs over all arrays. Significance of b2 concludes that it does, which means that some of the parents contain considerably more dominant genes than the others. This is shown by the standardized deviation (Figure 1) and W_r , V_r graph (Figure 2) for the two sub-sets of data. The W_r , V_r graph of sub-set I shows that Marquis is the most highly recessive parent as it lies farthest from the point of intersection of the W_r , V_r regression line and the limiting parabola while Khush-hal has considerably more dominant alleles as it occupies the nearest position. Figure 1 supports this conclusion by placing Khush-hal in the (—,—) quadrant, with a preponderance of dominant genes contributing towards low spikelet number, and Marquis in the (+,+) quadrant with an excess of recessive genes responsible for higher spikelet number. In sub-set II, Ciano is considered to be the most dominant parent, and according to Figure 1, also contributes to low spikelet number (—,— quadrant). Inconsistency of the ranking order of parents Khush-hal and Ciano is interesting to note (Figure 1). In sub-set I, Khush-hal showed a preponderance of dominant genes

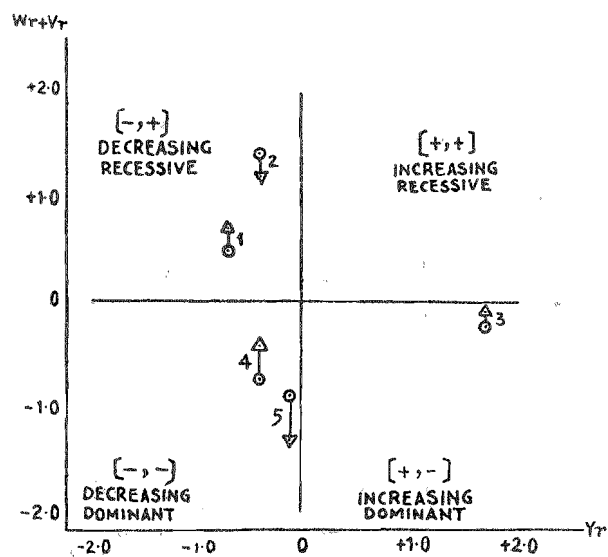


Fig. 3. Standardized deviation graph of parental measurements (Y_r) and parental order of dominance (W_r+V_r), for 1000-kernel weight from two sub-sets of F₂ diallel cross.
 O = $Y_r, (W_r+V_r)$ parental intercepts for sub-set I.
 Δ = $Y_r, (W_r+V_r)$ parental intercepts for sub-set II.

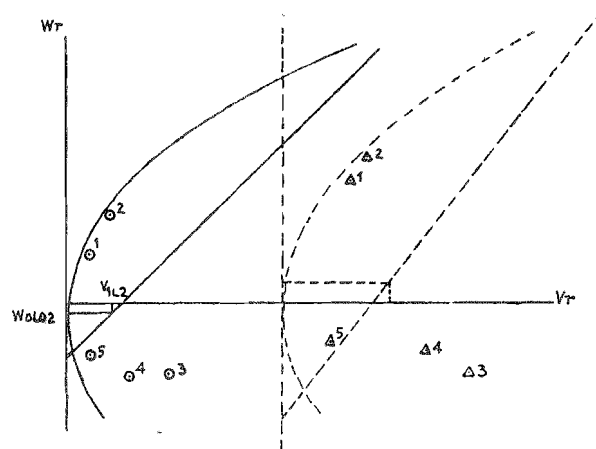


Fig. 4. V_r, W_r graph for 1000-kernel weight from two sub-sets of F₂ diallel cross respectively.
 O = V_r, W_r parental intercepts of sub-set I.
 Δ = V_r, W_r parental intercepts of sub-set II.

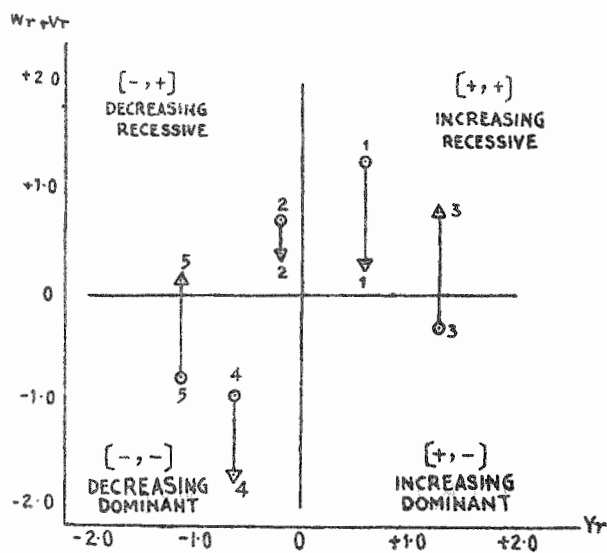


Fig. 5. Standardized deviation graph of parental measurements (Y_r) and parental order of dominance ($W_r + V_r$) for yield per plant from two sub-sets of F_2 diallel cross.

O = parental Y_r , ($W_r - V_r$) intercepts for sub-set I.
 Δ = parental Y_r , ($W_r - V_r$) intercepts for sub-set II.

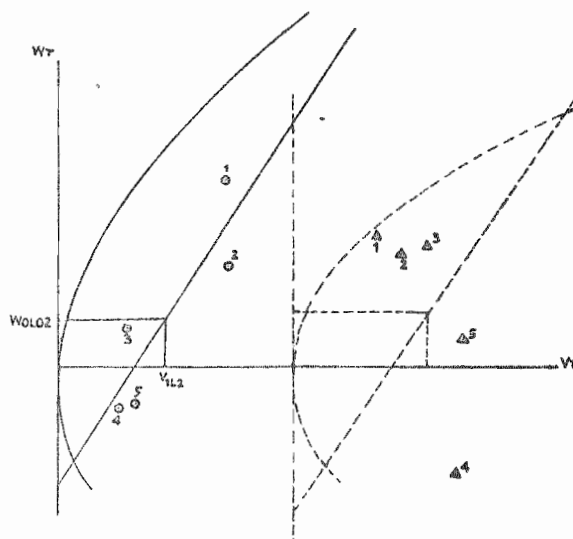


Fig. 6. V_r , W_r graph for yield per plant from two sub-sets of F_2 diallel cross.

O = V_r , W_r parental intercepts of sub-set I.
 Δ = V_r , W_r parental intercepts of sub-set II.

while in sub-set II it appeared to be highly recessive. Inia, on the other hand, was highly recessive in sub-set I, but changed to highly dominant in sub-set II. This change in ranking of the parents for order of dominance may be attributed to the effects of reciprocal differences between the two sub-sets.

For 1000-kernel weight, Inia is considered to have an excess of dominant genes with predominantly low kernel weight in both the sub-sets, while Chinook is regarded as the most recessive one contributing towards low kernel weight (Figure 3 and 4). Khush-hal and Ciano are categorized as the most highly dominant parents producing high (+, — quadrant) and low (—, — quadrant) kernel weight respectively in both the sub-sets. Marquis may be classified as the next parent most recessive to Chinook for low kernel weight. The parental order of dominance seem to be unchanged for both the sub-sets.

For yield, the W_r , V_r graph (Figure 6) reveals that Marquis contains a preponderance of recessive genes for high yielding capacity (+, + quadrant of Figure 5) and Ciano contains comparatively more number of dominant genes for low yielding capacity (+, — quadrant) for both the sub-sets. The ranking order of Khush-hal and Inia seem to be changed in the two sub-sets, both the parents being dominant in one sub-set (+, — and —, — quadrants, respectively) and predominantly recessive in sub-set II (+, + and —, + quadrants respectively), though their yielding capacity is not significantly changed.

In conclusion, partitioning the diallel table into two reciprocal sub-sets affects the array variances (V_r) and array parent-offspring covariances (W_r). This effect is reflected by the order of dominance and the proportion of positive to negative gene effects of the parental lines. Genetic components of variation such as D and h^2 are unaffected (as revealed from the values of $VOLO$ and $(MLI-MLO)^2$ in Table 6) in either sub-set because these statistics are purely additive and moreover, the value of the recurrent parent used in the arrays for computation of these second degree statistics is constant.

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